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Published in:
Journal of Avian Biology

DOI:
[10.1111/j.1600-048X.2009.04763.x](https://doi.org/10.1111/j.1600-048X.2009.04763.x)

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Document Version
Publisher's PDF, also known as Version of record

Publication date:
2010

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Citation for published version (APA):

Vezina, F., Dekinga, A., & Piersma, T. (2010). Phenotypic compromise in the face of conflicting ecological demands: an example in red knots *Calidris canutus*. *Journal of Avian Biology*, 41(1), 88-93.
<https://doi.org/10.1111/j.1600-048X.2009.04763.x>

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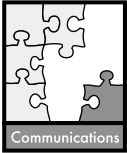
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Phenotypic compromise in the face of conflicting ecological demands: an example in red knots *Calidris canutus*

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Phenotypic flexibility is a phenomenon where physiological functions in animals are reversibly adjusted in response to ecological constraints. Research usually focuses on effects of single constraints, but under natural conditions animals face a multitude of restrictions acting simultaneously, and potentially generating conflicting demands on the phenotype. We investigated the conflicting demands of low temperatures and a low quality diet on the phenotype of a shorebird, the red knot *Calidris canutus*. We tested the effects of switching diet from a high quality trout food to low quality hard-shelled bivalves in captive birds acclimated to temperatures reflecting natural winter conditions. Feeding on bivalves generated a digestive constraint forcing the birds to increase the height and width of their gizzard by 66% and 71%, respectively, over 30 days. The change in gizzard size was associated with an initial 15% loss of body mass and a reduction in size of the pectoral muscles by 11%. Because pectoral muscle size determines summit metabolic rate (M_{sum} , an indicator of cold endurance), measured M_{sum} declined by 9%. Therefore, although the birds were acclimated to cold, gizzard growth led to a loss of cold endurance. We propose that cold-acclimated knots facing a digestive constraint made a phenotypic compromise by giving-up cold hardiness for digestive capacity. Field studies suggest that phenotypic compromises occur in free-living red knots as well and help improve survival.

Phenotypic flexibility is a complex phenomenon involving reversible changes of morphological structures or physiological function in adult animals in response to environmental challenges (Piersma and Drent 2003). Although the phenomenon has received a lot of attention in recent years (e.g. Piersma and Lindström 1997, Piersma and Drent 2003, McKechnie 2008), studies usually record phenotypic responses to one specific challenge at a time (e.g. diet, Starck and Kloss 1995, exercise, Deerenberg et al. 1998, reproduction, Wiersma et al. 2004, predation, van den Hout et al. 2006, temperature, Salvante et al. 2007, but see Rogowitz 1998, Hammond et al. 1994, Hammond and Kristan 2000, Johnson and Speakman 2001). Under natural conditions, however, animals routinely face several constraints simultaneously. When traits are affected by two or more ecological variables, these may generate opposite responses compared to when they would act separately.

Conflicting demands on phenotypic traits are well illustrated by aspects of the winter ecology of the *islandica* subspecies of the red knot *Calidris canutus*, a long distance migrant shorebird that routinely migrate the thousands of kilometers between its nonbreeding areas in Europe and its breeding grounds in the Canadian Arctic and Greenland (Piersma 2007, Buehler and Piersma 2008). Being the northernmost wintering subspecies of knots, *islandica* spend

the cold season on West European mudflats from France to Denmark as well as in estuaries of the UK and Ireland (Davidson and Wilson 1992). In the Dutch Wadden Sea, the area where birds were captured for the present experiment, February is the coldest month of the year with an average temperature of 3° C (based on data from 1971 to 2000, R. Netherlands Meteorol. Inst., Den Helder station). Average monthly temperatures vary between years, and February temperature can be as low as –3.5° C. Acute but rare cold spells have also been recorded with temperatures going down to –18.8° C. Furthermore, mudflats offer virtually no shelter from the typical winter wind and rain, which are significant additional chilling factors (Lustick and Adams 1977, Webster and Weathers 1988, Wiersma and Piersma 1994). The two ecological factors ‘shaping’ the knot’s phenotype during the winter period are operational temperature and diet (Wiersma and Piersma 1994, van Gils et al. 2003, 2005a, b, Vézina et al. 2006).

Heat production under cold stress in birds is essentially the result of shivering thermogenesis (Marsh and Dawson 1989, Dawson and O’Connor 1996, Hohtola 2004, Swanson 2010) and wintering shorebirds have been reported to gain body mass and increase pectoral muscle size when facing natural (Davidson et al. 1986a, b) and experimental (Kelly et al. 2002, Vézina et al. 2006) cold

environments. In knots, larger pectoral muscles were associated with higher maximal thermogenic capacity (summit metabolic rate M_{sum} , Vézina et al. 2006, 2007), an indicator of cold endurance (Swanson 2001, Swanson and Liknes 2006). Yet, so far experimental evidences are based only on studies where birds were acclimated to cold in the absence of food-related constraints (Kelly et al. 2002, Vézina et al. 2006).

Because soft-shelled preys such as shrimps or crabs are not available in winter, wintering red knots specialize on a diet of mollusks, especially bivalves (van Gils et al. 2003, 2005b). Prey are ingested whole and must be crushed in the muscular gizzard for the flesh to be digested. This puts a tremendous constraint on the digestive system. When facing experimental switches in diet from soft, highly digestible, trout food to hard-shelled blue mussels *Mytilus edulis*, knots can double the size of their gizzard within 10–15 d (Piersma et al. 1999, Dekinga et al. 2001). Because gizzard size is highly correlated with the size of the intestine (Piersma et al. 2003), this phenotypic change reflects a phenomenon affecting the whole digestive system. Interestingly, Dekinga et al. (2001) reported significant loss of body mass during the growth of the digestive organs. It follows that because the size of the pectoral muscles closely tracks body mass (Lindström et al. 2000, Dietz et al. 2007), and is positively related to thermogenic capacity in this species (Vézina et al. 2006, 2007), a loss of body mass would potentially lead to a loss of cold endurance during digestive organ growth. This can involve fitness costs if the loss of muscle mass occurs under conditions of severe cold (Dietz and Piersma 2007). However, current knowledge on diet-related adjustments in gut size of knots comes from experiments conducted in absence of a cold challenge.

This paper investigates conflicting demands on the phenotype by studying the effects of gizzard growth on body mass and pectoral muscle size and the associated consequences in terms of thermogenic capacity in cold acclimated red knots.

Methods

Experimental animals and protocol

Six captive red knots were available for this study. All birds were adult when captured in the Dutch Wadden Sea in Sept. 2007. They were maintained captive in the NIOZ shorebird facilities until the end of the experiment. The birds were allowed to acclimatize to captivity in outdoor aviaries (described in Vézina et al. 2006) while fed a natural diet of mudsnails *Hydrobia ulvae*, and water *ad libitum*. After 13 d, the diet was switched to trout food (Trouvit, Produits Trouw, France), which contains no hard material to crush and is highly digestible. Both *Hydrobia* and trout food diets are known to consistently result in small gizzards in captive knots (Dietz et al. 1999, Dekinga et al. 2001, Vézina et al. 2006). Twenty-one days into captivity, the birds were moved to a temperature-controlled indoor aviary (described in Vézina et al. 2006) where they were allowed to acclimatize to a temperature of 4° C for a period of 52 d before we triggered the growth of their digestive organs by changing their food to blue mussels. Summit metabolic rate

was measured by respirometry during the last week before the diet change following the protocol of Vézina et al. (2006, 2007).

We measured gizzard size and pectoral muscle thickness non-invasively by ultrasonography on the day we changed the diet from pellets to mussels (herein called d 1). The organs were measured according to Dietz et al. (1999). We then left the birds on the mussel diet for 30 d before measuring final values of M_{sum} . During this period each bird was weighed to the nearest 0.1 g once a day at 16:00 h and gizzard size and muscle thickness were measured in the morning every third d (except two cases where measurements were made 4 d apart) from d 9 to d 29.

Statistical analysis

We use a repeated measures design where each individual bird was used as its own control by comparing variables before, during and after a period of phenotypic adjustment to a change in diet. We therefore used repeated measure ANOVA in a general linear mixed model approach. The effect of day on organ variables were tested while considering the repeated nature of the experiment by including the random variable “bird number” in the model. For simplicity, and because we have no biological interest in this specific effect, we do not report statistical results for “bird number”. To investigate how the growth of the digestive organs may affect the size of the thermogenic machinery, we calculated the changes in gizzard size and the changes in pectoral muscle thickness between each of the measurement sessions. This provided a series of 7 measured changes per organ per individual. We then used the repeated measure ANOVA to compute least square means for each time point per organ measure (independent of individual effects, calculated with $n=6$ individuals per mean). Using regression analysis, we then investigated the relationship between the average change in gizzard height or width and the average change in pectoral muscle thickness. Effect of diet on M_{sum} was analyzed using paired t-test. Results presented are least square means \pm SE.

Results

Changing the diet from trout food to blue mussels had a dramatic effect on the size of the gizzard in cold-acclimated knots (effect of d on gizzard height: $F_{7,35}=38.2$, $P<0.001$, on gizzard width: $F_{7,35}=37.2$, $P<0.001$). Both gizzard measurements showed a steady increase with a plateau reached at d 26. By d 29, gizzard had increased in height by 66.0% and in width by 70.9% (Fig. 1a, b).

As expected, the change in diet also affected body mass ($F_{28,140}=4.8$, $P<0.001$). Body mass declined steadily for the first 7 d before stabilizing and showing a slow but variable increase for the rest of the experiment. At d 7, the birds had lost 14.7% of their mass while at day 29 the difference with d 1 was a loss of 11.0% (difference with average of the last 5 d was a loss of 9.3%, Fig. 1c). Confirming earlier reports that pectoral muscle mass tracks changes in body mass in this species (Lindström et al.

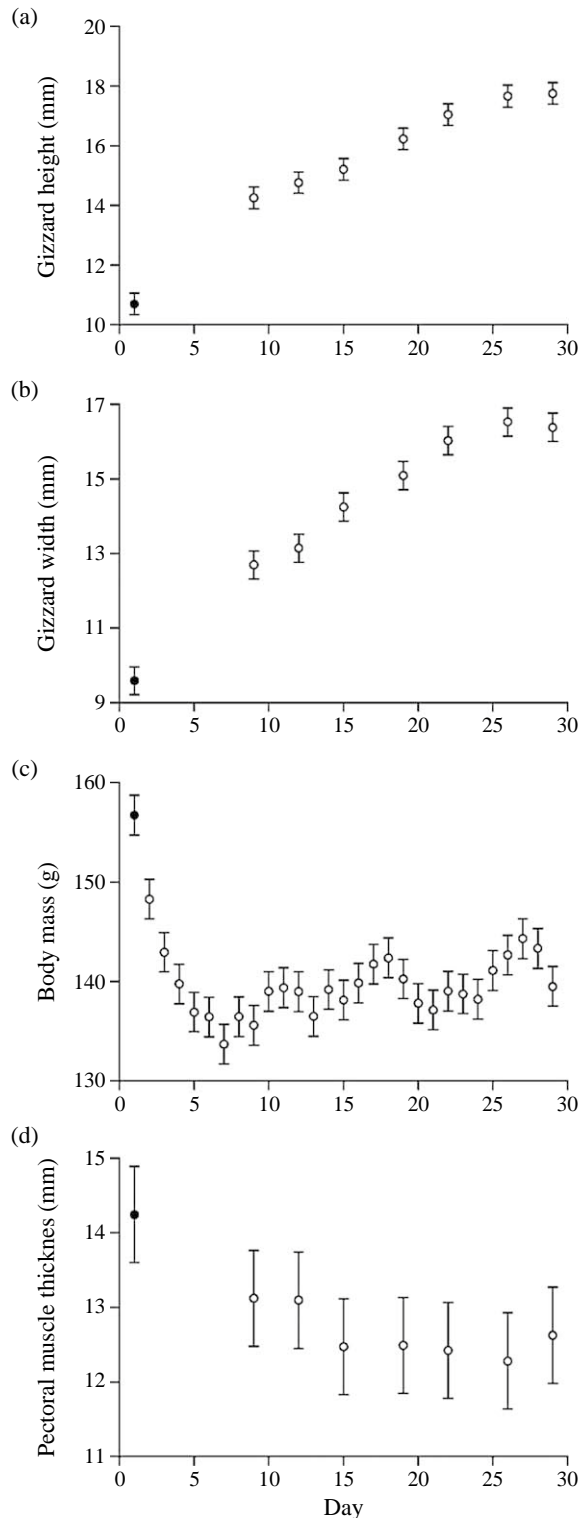


Figure 1. Changes in gizzard height (a), gizzard width (b), body mass (c) and pectoral muscle thickness (d) over 29 d following the change in diet from trout food to blue mussels. Filled symbols: values measured on the last d of the trout food treatment. Day 1=d of switch in diet.

2000), we also observed a decline in pectoral muscle thickness over time ($F_{7,35}=9.0$, $P<0.001$). The loss of muscle appeared rapid and stabilized by d 15. At the end of

the experiment, pectoral muscles were 11.4% thinner than at d 1 (Fig. 1d).

Pectoral muscle size varied in close relationship with the changes in size of the digestive organs. Indeed, both the average change in gizzard height and gizzard width were negatively correlated with the average change in pectoral muscle thickness (gizzard height: $r^2=0.66$, $F_{1,5}=9.6$, $P<0.05$, Fig. 2a, gizzard width $r^2=0.86$, $F_{1,5}=31.8$, $P<0.005$, Fig. 2b). In other words, during reconstruction of the digestive organs, the more the gizzard grew from one measure to another, the more the pectoral muscles shrank.

Pectoral muscles are the largest muscle group in the body and the main source of shivering heat production. Accordingly, the measured loss in pectoral muscle was associated with an 8.5% decrease in thermogenic capacity within individual (trout foot $M_{\text{sum}}=7.5\text{W}$, mussels $M_{\text{sum}}=6.8\text{W}$, $t_5=-2.1$, $P<0.05$).

Discussion

This experiment clearly showed the existence of a *phenotypic compromise* in knots when the conflicting demands of a cold environment and a low quality diet were combined. When

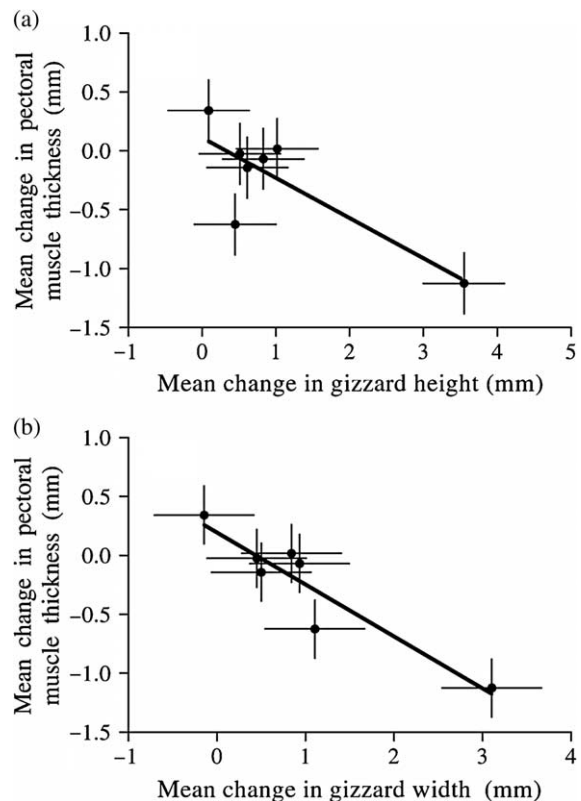


Figure 2. Relationship between the change in gizzard height (a), gizzard width (b) and the change in pectoral muscle thickness. Changes are calculated from one ultrasound measure to the next, providing 7 time periods. Data presented are least square means calculated from measurements on 6 individuals using a repeated measure ANOVA taking the time effect into account by including individual as a random variable. See text for details.

knots were switched from a high to a low quality diet, which requires large digestive organs to process bivalve shell matter (Dekinga et al. 2001), the birds showed a 66–71% increase in gizzard size over 30 d. This was associated with an initial period of energy deficit, illustrated by a rapid 15% loss of body mass during the first week. In parallel with the growth of the digestive organs, the pectoral muscles, which are the main avian thermogenic organs, decreased in size by 11%. As expected, birds also experienced a 9% decline in M_{sum} , and therefore cold endurance (Swanson 2001, Swanson and Liknes 2006). By the end of the experiment, the birds had recovered some body mass but pectoral muscle thickness remained constant without signs of regrowth. Therefore, knots had to give up cold hardiness to build up digestive capacity, even though they were maintained at a temperature representative of the coldest days of winter in the Wadden Sea (but without the wind chill effect that comes with their open environments, Wiersma and Piersma 1994).

Previous shorebirds studies reported increases in pectoral muscle mass and body mass in response to natural or experimental cold conditions (Davidson et al. 1986a, b, Kelly et al. 2002). We further showed that a gain in pectoral muscle leads to an improvement of thermogenic capacity and cold endurance in knots. In fact, knots acclimating to 4° C in absence of digestive constraint exhibit a 13% elevation in M_{sum} compared to birds maintained at thermoneutrality (25° C; Vézina et al. 2006, 2007). Here, however, we recorded a 9% decrease in M_{sum} when knots acclimated to 4° C reconstructed their digestive organs. Clearly, the conflicting demands for life in the cold and digestive capacity led to a phenotypic trade-off.

Trading-off cold endurance for the capacity to exploit a low quality diet may be a good strategy for knots as long as they are not facing acute cold for extended periods of time. When facing a low quality diet, the immediate need for larger nutritional organs presumably outweigh the insurance against possible but rare periods of high heat loss, which would require high thermogenic capacity and cold endurance. However, the cost of this strategy becomes clear when free-living birds are confronted with both constraints at the same time. Dietz and Piersma (2007) demonstrated that wintering knots that died of starvation during cold spells defended their capacity to acquire and digest bivalves, even when mudflats were frozen. This was achieved by maintaining the size of their gizzards and leg muscles at the expense of other body components that were catabolized for energy. Starving knots consumed over 60% of their pectoral muscle mass. Dietz and Piersma (2007) argued that such a loss of pectoral musculature impaired flight capacity, therefore increasing predation risks. Given the relationship between pectoral muscle size and maximal thermogenic capacity, we add to this reasoning that birds in such a state most likely experienced very low levels of thermogenic capacity and cold endurance, thus affecting their ability to survive the cold spell with which they were faced (see Dietz and Piersma 2007).

Another indirect line of evidence supporting our findings is provided by a study on the effects of shellfish dredging on survival of wintering red knot populations in

the Wadden Sea (van Gils et al. 2006). In recent years, possibly because of the action of dredging on sediment characteristics (Piersma et al. 2001), the quality of bivalves prey (measured in units of shell to flesh mass) declined to a point forcing wintering knots to increase mean annual gizzard size to cope with the need for extra shell-processing (van Gils et al. 2006). Van Gils et al. (2006) demonstrated that color-marked birds never seen again after release had undersized gizzards compared to birds known to have survived. Furthermore, these birds tended to have lower body mass, and thus presumably a lower condition. Based on our present findings, we suggest that the low body mass reflects the initial energy deficit during gizzard reconstruction. Because this leads to a loss of pectoral muscles and cold endurance, any birds in this situation in the wild would potentially be at risk in case of prolonged cold, rainy, windy periods, which is characteristic of this habitat in winter.

Vézina et al. (2006) demonstrated that captive knots kept at 4° C, in absence of diet constraint, acclimate to cold by increasing body mass and pectoral muscle size which leads to higher thermogenic capacity. Here we demonstrated that when the temperature constraint is combined with a low quality diet, birds trade-off cold hardiness for digestive function. That being said, living at winter-like temperatures is likely to require a certain minimum muscle size to support thermoregulatory needs. Given that daily energy intake when feeding on mussels is limited by gizzard size (van Gils et al. 2005a, b), we argue that minimal muscle size requirements could constrain gizzard growth rate in cold environments. Support for this hypothesis comes from an earlier experiment on red knots performed by our group. Dekinga et al. (2001) documented changes in gizzard size in a series of four independent switches in diet from trout food to blue mussels. Their birds were kept outdoor and experienced average ambient temperatures of 5.7° C, 8.9° C, 11.2° C and 10.2° C during the four periods of gizzard growth, respectively (data retrieved from R. Netherlands Meteorol. Inst., Den Helder station). Their birds were therefore exposed to temperatures 1.7–7.2° C higher than during the present experiment. Dekinga et al. (2001) reported an average rate of gizzard growth of 0.42 g/d and gizzard attaining final size within 2 to 9 d. Converting our size data to mass using their conversion equation, our birds experienced a rate of gizzard mass increase of 0.22 g/d and took 25 d to reach final mass (Fig. 1). Therefore, lower thermostatic costs at warmer temperatures could allow for faster gizzard growth and body mass recovery. However, caution is advised when making such comparison since difference in mussel quality between studies could also partly explain the results. Further studies involving different thermal regimes and diet qualities within a same experiment are needed to test this hypothesis.

Acknowledgements – This work was supported by a VENI grant to FV from the Netherlands Org. for Sci. Res. (NWO) and a NIOZ-operating grant to TP. We are grateful to Maarten Brugge for help with the birds and to Oliver P. Love and Katrina

G. Salvante who provided constructive comments on an earlier draft of this paper.

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